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Preferential Expression of Linear Enamel Hypoplasia on the Sectorial Premolars of Rhesus Monkeys (*Macaca mulatta*)

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ABSTRACT Three hundred and sixty rhesus macaque specimens at the Caribbean Primate Research Center were examined for evidence of linear enamel hypoplasia (LEH). A previously unreported intertooth pattern in LEH was observed. Defects occur preferentially on the sectorial premolar of both males and females. Relative to other teeth, the sectorial premolar exhibits more prominent defects and is more likely to exhibit multiple defects. This pattern is unlike the human intertooth LEH pattern and unlike patterns previously reported for monkeys and apes. These observations are discussed in the context of factors thought to influence the intertooth distribution of LEH in humans and in nonhuman primates. The authors reject crown height, the timing of crown development, and the duration of crown formation as factors contributing to the observed pattern and favor an explanation involving enamel thickness, perikymata spacing, and/or prism orientation. Am J Phys Anthropol 107:179–186, 1998. © 1998 Wiley-Liss, Inc.

Linear enamel hypoplasia (LEH) is a developmental defect of enamel appearing as one or more horizontal lines or grooves on the surface of a tooth crown (Goodman and Rose, 1990). The defect forms when physiological stress (such as febrile disease or poor nutrition) disturbs enamel matrix formation, resulting in a deficiency of enamel thickness (Goodman and Rose, 1990; Ten Cate, 1994). Although many anthropological studies have used LEH as a tool for assessing levels of stress in human populations, the use of this defect as a stress indicator in extant and extinct nonhuman primates is not widespread.

In order to make use of LEH as a stress indicator in nonhuman primates, basic descriptive research in the patterning of this defect across and within species, populations, and the tooth crowns themselves is needed. Most previous research in nonhuman primate LEH has focused either on interspecific variation in LEH incidence (Colyer, 1936, 1947; Moggi-Cecchi and Crovella, 1991; Schuman and Sognnaes, 1956; Skinner and Guatelli-Steinberg, 1997; Vitzthum and Wikander, 1988) or on LEH in the Hominoidea (Eckhardt, 1992; Jones and Cave, 1960; Moggi-Cecchi and Crovella, 1991; Skinner, 1986; Skinner and Roksandic, 1995; Skinner et al., 1995; Zhang, 1987). Less attention has been focused on LEH in the Cercopithecoidea, especially with respect to intertooth variation in LEH expression.

Moggi-Cecchi and Crovella (1991) found that within the Cercopithecoidea, enamel hypoplasia (defined as pits, lines, and grooves) reaches its greatest expression on

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the maxillary incisors and mandibular canines. Similarly, Vitzthum and Wikander (1988) observed that, in cercopithecoids, most defects occur on the anterior teeth. These patterns are like those observed in humans (Goodman and Armelagos, 1985) and African apes (Skinner, 1986; Vitzthum and Wikander, 1988), in which maxillary incisors and mandibular canines are most often affected. LEH variation among teeth presumably arises as a result of differences in developmental timing, crown formation time, crown height, and/or developmental canalization (Goodman and Armelagos, 1985).

Both Moggi-Cecchi and Crovella (1991) and Vitzthum and Wikander (1988) combined observations from several species in their cercopithecoid samples, making species-specific and population-specific patterns unobservable. By contrast, in this investigation, intertooth variation in the expression of LEH is studied in a single large population of rhesus macaques. A clear and unexpected pattern is observed: LEH is expressed preferentially on the sectorial premolar. This pattern is discussed in the context of factors thought to influence the distribution of LEH across the dentition.

MATERIALS AND METHODS

The Caribbean Primate Research Center in Puerto Rico maintains the large collection of Cayo Santiago rhesus macaque skeletons that formed the basis of this study (for a description of the Cayo Santiago rhesus macaque colony, see Rawlins and Kessler, 1986). Permanent teeth of 360 specimens (179 males, 181 females) were examined for evidence of LEH. Teeth were observed under diffuse lighting with a second, direct light source oriented obliquely to the specimen (see Goodman and Rose, 1990). A $\times 10$ hand lens aided in defect identification. If one-half or more of a tooth was not visible (due to wear, breakage, or partial eruption), it was considered to be unobservable and was not scored. Because LEH was observed along the honing surface of sectorial premolars, wear was an obvious problem. Sectorial premolars were not scored if one-half or more of their honing surfaces were covered with wear striae. The threshold for scoring LEH presence was set deliberately low to include mild stress events occurring during tooth development (Skinner et al., 1995). Hillson and Bond (1997:98) recently found that even small, microscopic furrows are "just as much indicators of disturbance to growth as ... large defects."

Defects were rated as either mild or pronounced based on their width and depth. It is not clear to what extent defect dimensions reflect the severity of stress events. Suckling et al. (1986) showed that when sheep are experimentally infected with nematodes, the severity of the systemic reaction influences the amount of missing enamel in the resulting hypoplastic lesions. On the other hand, Hillson and Bond (1997) recently demonstrated that defect width and depth are strongly influenced by the position of the defect on the crown (as a consequence of crown growth geometry). Thus, no assertions will be made here about the meaning of defect dimensions. Instead, the defect rating system employed is meant simply to give an indication of defect prominence.

Because there are no side differences in LEH expression (df = 1, chi-square = 0.0135, $P < 0.9075$), left and right teeth are pooled in the analysis. An individual is scored as positive for the defect if LEH occurs on at least one antimeric pair. This convention maximizes the possibility that the stress events precipitating defect formation are systemic rather than local (Goodman and Rose, 1990). Intertooth variation in LEH expression is analyzed only for individuals scoring positive for LEH, making the effective sample size 61: 43 females, 18 males. There are fewer males than females scoring positive for the defect because more males than females had worn sectorial premolars that were scored as unobservable. LEH presence on a tooth is defined as the occurrence of one or more defects and absence as a lack of any defects.

Both chi-square tests and generalized estimating equations (GEEs) are used to analyze the results. The starting point for the GEE analysis is a generalized linear model, using logistic regression to model LEH presence vs. absence (a binary response variable) and Poisson regression to model the number of hypoplastic defects (a count response variable) (SAS Institute Inc., 1996).

TABLE 1. Percent of tooth class in each jaw exhibiting defects in 61 individuals scoring positive for LEH

Tooth type	Total teeth in lower jaw sample	Percent of teeth affected in lower jaw	Total teeth in upper jaw sample	Percent of teeth affected in upper jaw
I1	111	11.7	109	15.6
I2	108	3.7	112	3.6
C	104	25.0	108	0.9
P3	105	80.0	120	0.3
P4	119	5.0	119	0.0
M1	116	0.0	122	0.0
M2	122	1.6	119	0.8
M3	98	0.0	88	0.2

The regression procedure fits the linear model to the data by maximum likelihood estimation of the model's parameters (SAS Institute, Inc., 1996).

To the generalized linear model, the GEE methodology adds the ability to analyze correlated data sets, such as the presence or absence of LEH on the teeth of a single individual. The GEE procedure makes weak assumptions about the actual correlation; it employs a working correlation matrix that approximates the average dependence among repeated (or clustered) observations over all subjects (Stokes et al., 1995). By taking the correlation into account, GEEs are sensitive to detecting differences in the LEH expression of different teeth within the same specimen. The GEE procedure provides an odds ratio that specifies the chances of obtaining defects on one tooth vs. another. GEEs have become "an important strategy for the analysis of correlated data which may arise from longitudinal studies...or clustering in which measurements are taken on subjects who share a common characteristic" (SAS Institute Inc., 1998). In the present analysis, the correlated data are LEH counts (or presence/absence) on an individual's teeth; their shared characteristic or cluster is the individual specimen to which the teeth belong.

RESULTS

Presence/absence

Table 1 shows, for the combined sample (males plus females), the percent of teeth with LEH for each tooth type in individuals scoring positive for the defect. Figure 1 is a histogram of these frequencies.

A presence vs. absence chi-square analysis for the combined sample reveals highly significant differences among all teeth (df = 11, chi-square = 741.3, $P < 0.001$). Upper molars are grouped into one category and lower molars into another in order to maintain adequate cell size. Of all the presence cells in the chi-square table, the lower P3 has the highest actual count relative to its expected count; molars have the lowest.

GEE analysis of presence/absence is conducted on the lower canine, lower incisors, lower premolars, and upper central incisor (other teeth had too few defects to be included). Relative to these teeth, the lower P3 shows a significantly greater occurrence of LEH. Table 2 shows the results of the GEE analysis. The likelihood of defect presence on the lower P3 relative to other teeth affected with LEH is given in the second column. A GEE analysis conducted on males and females separately reveals similar relationships between the lower P3 and other affected teeth (see Tables 3, 4;) (lower P4s could not be included because they had too few defects.) The GEE analyses of intertooth differences in the presence of LEH reveal that within an individual the lower P3 has a significantly greater likelihood of having a defect than any other tooth.

Defect counts

Table 5 displays the raw data for the number of teeth showing zero, one, or multiple defects in the combined sample. The lower premolar is often affected with multiple defects.

The number of defects exhibited by lower canines and maxillary central incisors is compared to that of lower P3s. GEE analysis of the combined sample shows that lower P3s are 6.23 times more likely to have a greater number of defects than upper central incisors (df = 1, chi-square = 63.1, standard error = 0.2303, $P < 0.0001$) and 3.96 times more likely than the lower canines (df = 1, chi-square = 50.0, standard error = 0.1946, $P < 0.0001$).

Separate analyses of females and males reveal a similar relationship. For females, the lower P3 is 14.60 times more likely to have a higher number of defects than the upper central incisor (df = 1, chi-square =

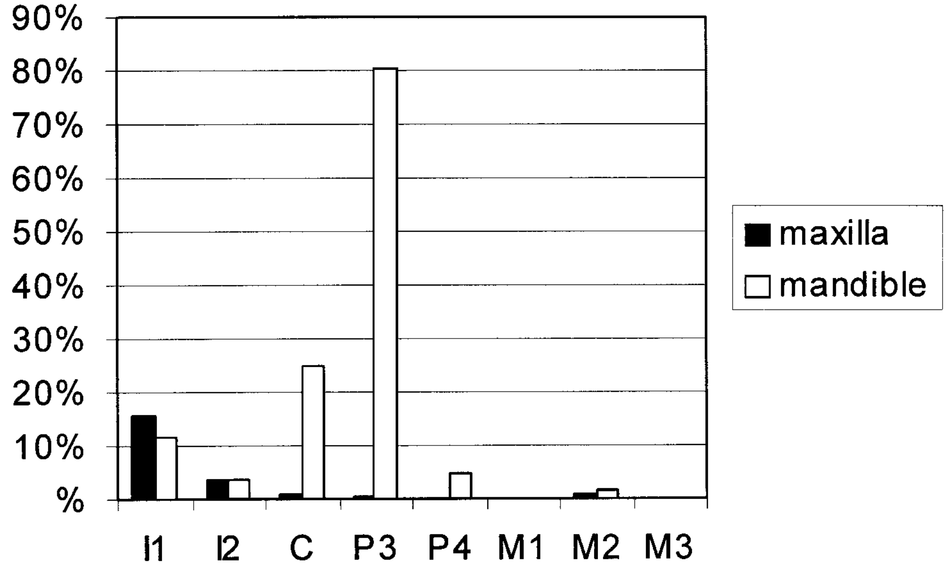

Fig. 1. Percent of tooth type exhibiting one or more defects in individuals scoring positive for LEH (actual percents given in Table 1).

TABLE 2. Presence of LEH[1] on the lower P3 relative to other teeth

Tooth	Rate at which LEH is more likely to occur on P3 relative to tooth listed at left	df	Standard error	Chi-square value	*P* value
Upper I1	21.65	1	0.3595	73.2	0.0001
Lower I1	30.15	1	0.3830	79.1	0.0001
Lower I2	104.00	1	0.5649	67.6	0.0001
Lower C	12.00	1	0.3329	55.7	0.0001
Lower P4	75.33	1	0.4848	79.5	0.0001

[1] Sexes combined (61 individuals scoring positive for LEH).

TABLE 3. Presence of LEH on the lower P3 relative to other teeth in females[1] only

Tooth	Rate at which LEH is more likely to occur on P3 relative to tooth listed at left	df	Standard error	Chi-square value	*P* value
Upper I1	63.92	1	0.5824	51.0	0.0001
Lower I1	22.90	1	0.4246	54.4	0.0001
Lower I2	139.00	1	0.7668	41.4	0.0001
Lower C	10.00	1	0.3784	37.0	0.0001

[1] Forty-three individuals scoring positive for LEH.

40.6, standard error = 0.4208, $P < 0.0001$) and 3.29 times more likely than the lower canine (df = 1, chi-square = 29.9, standard error = 0.2178, $P < 0.0001$). For males, the lower P3 is 3.24 times more likely to have a higher number of defects than the upper central incisor (df = 1, chi-square = 15.3, standard error = 0.3005, $P < 0.0001$) and 7.20 times more likely than the lower canine (df = 1, chi-square = 20.0, standard error = 0.4410, $P < 0.0001$). Thus, the GEE analyses for defect counts demonstrate that within an individual the sectorial premolar is more likely than any other tooth to exhibit multiple defects.

Defect prominence

The greatest defect category assigned to any of the defects on a tooth is the tooth's LEH prominence value. Therefore, a tooth itself is characterized as having pronounced LEH if one or more of the tooth's defects are classified as pronounced.

The LEH prominence values of the upper central incisors, lower canines, and lower P3s are compared with each other in a chi-square test. There are significantly different LEH prominence values for these teeth (df = 4, chi-square = 117.3, $P < 0.001$). In the pronounced category, the lower P3 alone has a higher actual cell count (37) relative to

TABLE 4. Presence of LEH on the Lower P3 relative to other teeth in males[1] only

Tooth	Rate at which LEH is more likely to occur on P3 relative to tooth listed at left	df	Standard error	Chi-square value	*P* value
Upper I1	9.29	1	0.6465	11.9	0.0006
Lower I1	78.75	1	0.9116	22.9	0.0001
Lower I2	78.13	1	0.9112	22.6	0.0001
Lower C	21	1	0.7113	18.3	0.0001

[1] Eighteen individuals scoring positive for LEH.

its expected cell count (15). The chi-square analysis could not be conducted for males (because of low cell counts), but the comparison for females is similar to that for the combined sample. For females, differences in prominence are significant (df = 4, chi-square =114.0, $P < 0.001$), and the lower P3 has a higher actual pronounced cell count (31) than is expected (12).

Figure 2 is a photograph of a pronounced defect on a left lower P3 of a male rhesus macaque. No LEH was observed on the left lower canine. Figure 3 is a closeup of a pronounced defect on a left lower P3 of a second rhesus male.

DISCUSSION AND CONCLUSIONS

The data presented here demonstrate a pattern of LEH distribution within the dental arcade that has not previously been noted in a nonhuman primate species. The sectorial P3 exhibits LEH preferentially, is more likely to have multiple defects, and has defects that appear more pronounced in that they are deeper and wider than those of other teeth. Moggi-Cecchi and Crovella (1992) noted that the P3s of cercopithecoids often showed LEH. However, these authors reported that cercopithecoid maxillary incisors and mandibular canines were more often affected than lower P3s. Previous researchers may not have noted the pattern described in this paper because this study is the first to have examined intertooth LEH variability in such large numbers of rhesus monkeys.

Moggi-Cecchi and Crovella (1991) and Goodman and Rose (1990) consider canine teeth to be more vulnerable to LEH as a result of their crown height. The deposition of large amounts of enamel on the high canine crown is thought by these authors to make ameloblasts more vulnerable to disruption. In the view of Skinner et al. (1995), canine teeth simply have a greater opportunity to record disruptions since they form over longer time periods than other teeth. In light of these explanations, the preferential expression of LEH on the mandibular P3 of rhesus monkeys is interesting. There are currently no published data on the calcification times of lower P3s and canines in rhesus monkeys. However, mandibular P3s and canines take approximately the same amount of time to calcify in pig-tailed macaque (*M. nemestrina*) females; in *M. nemestrina* males, lower P3s form over a shorter time period than lower canines (Sirianni and Swindler, 1985). If tooth development in *M. mulatta* is similar to that of *M. nemestrina,* then the duration of calcification does not offer a clue as to preferential P3 LEH expression in rhesus monkeys. An explanation in terms of crown height is also untenable. In the females of this rhesus sample, the mandibular P3 has a slightly shorter crown height (an average of 8.6 mm over 21 specimens) than the mandibular canine (an average of 9.6 mm over 18 specimens). In males, the average mandibular canine crown height is 15.4 mm (19 specimens), and the average lower P3 crown height is 13.2 mm. (These are unpublished measurements taken by the first author on this sample.)

Although it is possible that lower P3s are calcifying at times when other teeth are not and perhaps when stress events are occurring more frequently, this does not seem likely for the following reason. In *M. nemestrina* females, the lower P3 and mandibular canine form simultaneously (Sirianni and Swindler, 1985). Assuming that female rhesus monkeys have a calcification schedule similar to that of female pig-tailed macaques, one would expect that the lower P3 and mandibular canine would exhibit defects equally if they were equally susceptible. However, in the female rhesus sample studied here, the lower P3 is ten times more likely to exhibit defects than the lower canine. These findings are exactly opposite those reported by Condon (1981) for hu-

TABLE 5. Number of teeth exhibiting 0, 1, or multiple defects[1]

	Number of defects in lower jaw					Number of defects in upper jaw		
Tooth	0	1	2	3	4	0	1	2
I1	98 (88.3)	9 (8.1)	4 (3.6)	—	—	92 (84.4)	12 (11.0)	5 (4.6)
I2	104 (96.2)	2 (1.9)	2 (1.9)	—	—	108 (96.4)	4 (3.6)	—
C	78 (75.0)	21 (20.2)	3 (2.8)	2 (2.0)		107 (99.1)	—	1 (0.9)
P3	21 (20.0)	49 (46.7)	25 (23.8)	7 (6.7)	3 (2.8)	117 (97.5)	3 (2.5)	—
P4	113 (95.0)	6 (5.0)	—	—	—	119 (0.0)	—	—
M1	116 (100)	—	—	—	—	122 (0.0)	—	—
M2	120 (98.4)	2 (1.6)	—	—	—	118 (99.2)	1 (0.8)	—
M3	98 (0.0)	—	—	—	—	86 (97.7)	2 (2.3)	—

[1] Percents in parentheses.

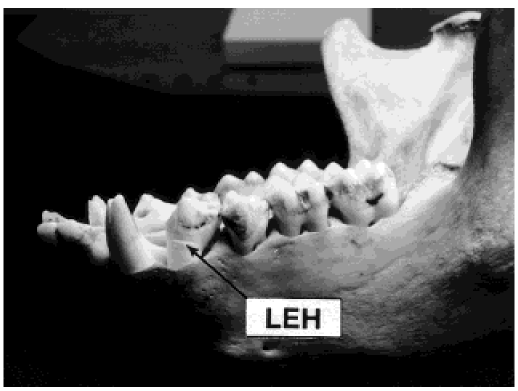

Fig. 2. Pronounced defect on the left mandibular P3; defects absent on the lower left canine.

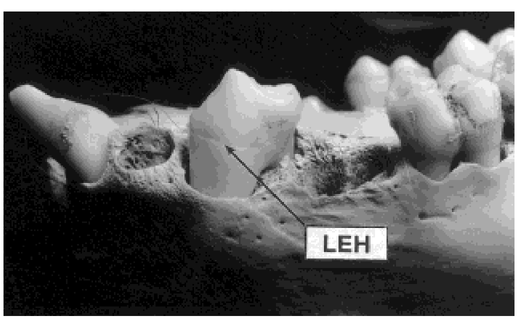

Fig. 3. Pronounced defect on the left mandibular P3.

mans. In comparing 30 matched mandibular canines and lower P3s, Condon (1981) found defects on the canine that could not be matched to any defects on the premolar, despite that fact that these teeth develop simultaneously in humans.

If the duration of crown formation, crown height, and the timing of crown development are not involved, then what factors may explain the rhesus pattern? A number of characteristics of the sectorial premolar may make it more susceptible to defect expression. The tooth is highly angled because of its functional relationship as a "whetstone" for the upper canine. Perhaps the enamel prisms are oriented to the enamel surface in such a way as to make defects more likely to appear. Goodman and Armelagos (1985) explain human LEH intratooth patterns in these terms. Alternatively, perikymata spacing may differ between mandibular canines and P3s, perhaps influencing defect definition. Hillson and Bond (1997) have shown that defect dimensions vary within tooth crowns mainly because of variation in the spacing of perikymata grooves. In addition, Goodman and Armelagos (1985) suggest that ameloblasts forming enamel at a high rate may be more vulnerable to disruption than ameloblasts with less taxing enamel production schedules. Recently, Washburn (1997) demonstrated that the sectorial premolars of both male and female old world anthropoids are covered with a thick layer of enamel (presumably related to the honing function of this tooth). If ameloblasts are secreting a thicker layer of enamel on the sectorial P3 than they are on the mandibular canine during the same span of time,

then ameloblasts of the lower P3 might be more easily disrupted.

Goodman and Rose (1990) argue that developmental canalization may explain the high rate of enamel defects on functionally key teeth such as the teeth of the sectorial complex (maxillary canine, sectorial premolar). If development is highly canalized in functionally key teeth, the sectorial complex may be unable to alter its developmental path in response to systemic stress. Garn et al. (1966) noted that the second incisor, canine, and first premolar show similar patterns of sexual dimorphism, indicating that these teeth develop as part of a canine growth field. The canine growth field could help explain why the lower canine and sectorial premolar both have elevated defect frequencies, but it does not help elucidate the cause(s) of preferential LEH expression on the sectorial premolar.

It is not clear to what extent the observed pattern characterizes other populations of rhesus monkeys or other species of cercopithecines. This population differs from feral populations of rhesus monkeys in that it is provisioned, but we can see no reason why provisioning would influence the intertooth distribution of defects. Peak infection by the nematode parasite *Strongyloides* occurs in yearling and 2-year-old Cayo Santiago monkeys (Kessler et al., 1984). While this age of infection overlaps with the time span for sectorial premolar calcification, it also overlaps with that for the lower canine, based on calcification schedules in *M. nemestrina* (Sirianni and Swindler, 1985). As emphasized earlier, differences in calcification timing cannot explain the greater expression of LEH on the sectorial premolar relative to the lower canine.

Unpublished data by the first author on small samples of other LEH-positive cercopithecines indicates that similar patterns can be found in *M. fascicularis* (N = 8) and in *Papio* (N = 13). In the *M. fascicularis* sample, the mandibular first incisor is followed by the sectorial premolar in having the greatest incidence of LEH. In the *Papio* sample, the sectorial premolar is second to the maxillary central incisor in being most often affected. Interestingly, in several of the *Papio* specimens, pronounced defects occurred on the sectorial premolar, while more mild defects (or no defects at all) were found on the lower canine. The greater expression of LEH on the sectorial premolar relative to the mandibular canine in these samples of *M. fascicularis* and *Papio* requires further investigation in much larger samples (and a species-by-species examination in *Papio*).

An investigation into the causes of sectorial premolar LEH susceptibility in rhesus monkeys may be able to further our understanding of the reasons teeth vary in their ability to reflect systemic stress events. For reasons explained above, we believe that differences in crown height, the duration of crown formation, and developmental timing are not likely explanations of the heightened expression of LEH on the sectorial premolar relative to other teeth. Instead, we favor an explanation involving prism orientation, enamel thickness, perikymata spacing, and to a lesser extent developmental canalization. Currently we cannot discern the relative contribution of these factors, but future research could help illuminate these potential causes. Prism orientation and enamel thickness could be examined by comparative histological analysis of mandibular canines and P3s. Comparison of perikymata groove spacing on the mandibular canine and P3 would illuminate this potential explanation.

Whatever the cause(s), these data have important practical applications to the study of LEH in nonhuman primates. It is common practice for LEH researchers to focus only on teeth most likely to exhibit the defect. Therefore, when time is limited, researchers often examine only the mandibular canines and maxillary incisors for LEH (as recommended by Goodman and Rose, 1990). Because large samples of each species of nonhominoid primates have yet to be studied for LEH, there is a possibility that intertooth patterns will vary from species to species. Thus, as is evidenced by this study, if one were to examine only maxillary incisors and mandibular canines in nonhuman primates, a substantial number of defects could be missed, resulting in an underestimation of LEH frequencies. Until more basic research on the intertooth distribution of LEH in nonhuman primates is conducted, it will be important for researchers using LEH as a

stress indicator to examine all teeth of the permanent dentition.

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